IS THE GREAT WHITE HERON A GOOD SPECIES?

BY ERNST MAYR

THE heron family contains many interesting and puzzling cases of aberrant plumages. Examples from the North American herons are the Reddish Egret (*Dichromanassa rufescens*), with a normal and a white plumage, and the Little Blue Heron (*Florida caerulea*), with an immature white and an adult blue plumage. During my travels in the South Seas I saw almost daily individuals of the Reef Heron (*Egretta sacra*) which has a white color phase in addition to a normal gray one. When I first heard of the Great White Heron (*Ardea occidentalis*), I was certain that this so-called species was nothing but a locally distributed color phase of the Great Blue Heron (*Ardea herodias*), but then I became uncertain. It is museum workers like Ridgway and me who are inclined to consider the Great White Heron as conspecific with the Great Blue, while many of the naturalists who have studied them in the field considered these two forms good species. Holt (1928) presented the evidence in favor of the specific distinction of the Great White Heron so convincingly that his thesis was adopted in the Check-List of the American Ornithologists' Union and by the great majority of subsequent writers.

Yet, much as has been written about the Great White Heron, it has never been studied from a modern point of view. The new systematics, for which the population is the basic unit, always asks two questions when comparing two similar morphological types:

(1) Are individuals of these types merely divergent members of a single population, or are there in fact two? In the present case: Are the Great White Herons merely albino individuals of the Great Blue Heron, or do they form a separate population?

(2) If it is a separate population, is it reproductively isolated? If this question is answered with yes, the population is considered a good species. It is a subspecies, however, if it freely interbreeds with other populations.

First Question. What is the evidence for the alternative "albino individuals versus a discrete population"? Holt (1928) cites a number of points, which he considers as proof of the "population" character of the Great White Heron:

(1) Whiteness. "It is a pure white bird." This, of course, does not prove specific distinctness, because it is equally true for the white color of such unquestioned color phases as that of the Reddish Egret and Reef Heron.

(2) Bill. "The Great White Heron has a relatively larger bill than Ward's Heron." To determine the validity of this statement I have determined the bill index (length of the bill in per cent of wing length) in eleven adults of *occidentalis* and in fifteen adults of *Ardea herodias wardi*. This index is as follows:

occidentalis: 28.7, 29.1, 29.6, 31.0, 31.1, 31.5, 31.8, 33.0, 33.1, 33.9, 35.2. Mean: 31.6.

wardi: 27.5, 28.3, 28.7, 28.7, 28.9, 28.9, 29.4, 29.7, 29.8, 30.5, 30.5, 30.9, 31.1, 32.3. Mean: 29.7.

These figures show that of the 26 measured birds 20 are in the zone of overlap. Two *wardi* have a shorter bill than any *occidentalis*, and four of the latter a relatively longer bill than any *wardi*. There is thus an average difference in the relative length of the bill, but much overlap.

(3) Plumes. "The occipital plumes of *occidentalis* are reduced or absent." There can be no argument about this fact, only about its interpretation. Other cases are known, where albinos differ in feather structure from wild color birds. Yet, the evidence in the present case is rather overwhelming in favor of the assumption that the shortness of the occipital plumes is a population character of the Key West birds as compared to Florida mainland birds, rather than a by-product of whiteness in white individuals.

Our first question then can be answered with fair assurance: The Great White Herons are not merely albino specimens of Ward's Heron, but form a mangrove population in the Key West area which differs from Ward's Heron on the mainland not only by the white coloration, but also by shorter plumes and an average larger bill. This agrees with the findings of Holt and other recent investigators.

Second Question. What is the taxonomic status of this population? Is it a good species or is it an island subspecies of the Great Blue Heron?

Holt came to the conclusion that it was a good species and this conclusion has been accepted by the A.O.U. Check-List Committee. The arguments cited in favor of this decision are three:

(1) There is a behavior difference between the two kinds of herons. "The Great White Heron is a much shyer bird than the Great Blue." This observation of the older authors is not confirmed by more recent investigators. Sprunt, Robert Allen, Dan Beard, and others have written me that the shyness of these herons is directly proportional to the amount of persecution they suffer. Formerly, the Great White Herons were exposed to the unmerciful depredations of the Key West sponge fishermen. Since their protection they have

become much less shy. Whether or not shyness is always an "acquired" characteristic of a population or at least in part innate, is still disputed.

(2) They differ in their ecology. "The Great White Heron is a maritime species. The Great Blue is a fresh water bird." Again the assertion is not correct. To be sure, the Great White Heron is undoubtedly a salt water population. However, there are also many salt water populations of the Great Blue Heron, particularly along the coasts of the Gulf of Mexico, all the way from Florida to Mexico, and perhaps in the West Indies.

(3) "The two species nest side by side in Florida Bay and on the Key West Islands." This is the most difficult statement either to prove or to disprove. Additional facts need to be collected. Yet, there is already a great deal of evidence available that is highly suggestive:

(a) Many pairs have been found of which one parent was white, the other blue; among the young in many nests there have been both white and blue birds.

(b) An intermediate plumage type is known, the so-called "Würdemann's Heron." These intermediates are extremely variable. Some are entirely white-headed and otherwise very pale. Others appear indistinguishable from the Great Blue Heron except for having the occipital plumes shorter and with more white. It would be impossible to distinguish such birds in the field from Ward's Herons.

(c) All presumed "Ward's Herons" collected by Holt on the islands of Florida Bay turned out to be Würdemann's Herons when subsequently carefully examined in the museum (Holt, 1928).

(d) The only "Ward's Heron" from the Keys, examined by me, turned out to be a winter visiting Great Blue Heron from the north. In fact, I do not know of the existence in any museum of a single breeding specimen of pure Ward's Heron from the Florida Keys. However, so many so-called Ward's Herons have been observed in Florida Bay that their presence there can hardly be disputed.

(e) Dimorphic populations of the Great Blue Heron are known from the West Indies (Cuba, Isle of Pines, Jamaica) and Yucatan. In fact, an occasional white or *würdemanni*-like bird may occur anywhere within the range of the Great Blue Heron (see local records in several of the states north and west of Florida, often recorded as Great White Herons, rather than as albinos).

The cumulative weight of these five points of evidence is very strongly in favor of accepting *occidentalis* as a dimorphic subspecies of the Great Blue Heron, localized in the Florida Keys.

THE HISTORY OF THE GREAT WHITE HERON

In view of wide distribution of the Great Blue Heron on the mainland of America, without conspicuous geographic variation, it would seem legitimate to ask, how the very distinct dimorphic race of the Florida Keys evolved. Evidently this leads into the realm of speculation. We know that other dimorphic populations of this species (of smaller body size) occur on some of the Greater Antilles, although, here, the percentage of white birds in the population is comparatively small. There is little doubt that *occidentalis* is derived from such a dimorphic West Indian population. What we do not know, and probably never will, is whether the founders of the Florida Key population were, by chance, white and thus gave rise to a prevailingly white population or whether the white gene had a superior survival value on its genetic background in the ecologically distinctive environment of the Florida Keys. The "isolation effect" (Mayr, 1954) might have played a role in this change. Regardless of the reasons, the fact remains that in the Key area an endemic population developed consisting predominantly of white birds. This population appears to have been at one time quite effectively isolated from mainland birds, possibly because of some of the Pleistocene changes of climate and sea level. During this isolation genetic changes occurred which now find their visible expression in an enlargement of the bill, a reduction of the occipital plumes, and (as we shall presently see) in the acquisition of genes modifying the blue plumage from the Great Blue type in the direction of the Würdemann type.

In due time the isolation broke down and the Key population came again in contact with the mainland population of the Great Blue Heron (*wardi*). This occurred particularly on the inner Keys and on the islands of Florida Bay. There seems to be an increasing infiltration of genes from the mainland onto the islands of Florida Bay. It is here that observers most often see birds that seem to be *wardi*. R. P. Allen tells me that according to his recollection, on the outer Keys, where the gene infiltration from the mainland is not so pronounced, Würdemann's Herons tend to be more often of the extreme type (white head, very pale) than on the inner Keys of Florida Bay.

Here we are up against an as yet unsolved problem. The great variability of so-called Würdemann's Heron and the field observations of mixed white-blue pairs show clearly that *occidentalis* mixes with "*wardi*." However, what we do not know yet is the answer to this simple question: Do *occidentalis* and mainland birds hybridize in

this zone only occasionally or do they interbreed at random in their zone of contact?

This question, which corresponds closely to the Snow Goose—Blue Goose problem, can be solved only by field observation. Quantitative studies must be made on islands in the contact zone, that will show whether the frequency of mixed pairs corresponds to that expected by chance or is lower. Some casual observations by correspondents of mine suggest that possibly there is a tendency among blue birds to mate with blue birds, and of white to mate with white. But to say anything further would be pure speculation. The time has come for solid field work. The problems that need to be solved are the following:

(1) Study of variability of *würdemanni* on the Keys. Apparently they vary from almost *wardi*-like birds (with shortened plumes) to "extreme" *würdemanni* with much white in the plumage.

(2) The ratio of blue to white birds should be determined on some of the Keys, particularly inner and outer Keys. These censuses are most important. Is there a clinal increase in the percentage of blue birds toward Florida?

(3) The study of mated pairs. Is it true that there is no random mating, but a preponderance of matings of blue birds with blue birds and of white birds with white birds?

(4) Is there a difference in the breeding seasons of blue pairs and white pairs found on the same island?

(5) Are there any nests in which both parents are white, but some of the young are blue? Or, both parents blue and some of the young white?

THE GENETICS OF *Ardea occidentalis*

The older literature gave an altogether erroneous picture of the genetic situation. It stated that the white "species," *Ardea occidentalis*, met in the Keys the blue "species," *Ardea herodias* (in the subspecies *wardi*), and produced an intermediate hybrid, Würdemann's Heron. The true facts appear to be quite different. Since white as well as blue young are often found in nests, attended by a white and a blue parent, it is evident that a fairly simple mode of Mendelian inheritance is involved. The population of the Florida Keys is dimorphic, with a vast preponderance of white birds. The blue individuals of this population are not "normal" blue birds of the mainland type, but are, as Holt found out, more or less of the Würdemann type. There is good indirect evidence for the existence of a continuous inflow of blue genes from the mainland into the inner

Keys, resulting in an increased percentage of blue birds in this area and in the production of blue birds in which the "extreme" Würdemann characters are minimized.

In order to translate this information into the terminology of formal genetics we have to know first whether white or blue color is dominant. Mixed matings of white and blue birds do not give us this information. If both types of young are found in the nest and if white is dominant (white = W; blue = ww), such a mating would have the constitution Ww (white) × ww (blue). If blue were dominant (blue = B; white = bb), the genetic constitution of the parent birds would be: bb (white) × Bb (blue). Such back crosses of heterozygotes can shed no light on the question of dominance. What we need are cases where a cross of two similarly colored birds produces two kinds of offspring. This is possible only if both parents are heterozygotes (Ww or Bb). If both parents are white and yet produce white and blue young, then white (W) is the dominant gene, according to the formula: Ww × Ww = WW and Ww (white) and ww (blue). If both parents are blue, and yet produce blue and white young then blue (B) is the dominant gene according to the formula: Bb × Bb = BB and Bb (blue) and bb (white).

Are such pairings known? Mr. A. Sprunt writes me that he believes he remembers several cases where two white parents produced blue offspring. If this recollection is valid, it would prove that the white gene is dominant.

It is evident that this genetic model does not provide an explanation for Würdemann's Heron, with its pale color, shortened plumes, and lengthened bill. It is highly probable that these characters are produced by a whole complex of modifying factors which evolved in the Key population during its isolation. If, at the risk of over simplification, we should use the genetic symbol M for this modifying complex, and assuming white (W) to be dominant, we would have the following constitution for the three kinds of Herons:

Great White Heron	WW	MM
	Ww	Mm
		mm
Würdemann's Heron	ww	MM
		Mm
Great Blue Heron (Ward's)	ww	mm

It seems to me that such a genetic model is consistent with the facts as known up to the present.

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